



Impact of an invasive herbivore and human trampling on lichen-rich dry grasslands: Soil-dependent response of multiple taxa

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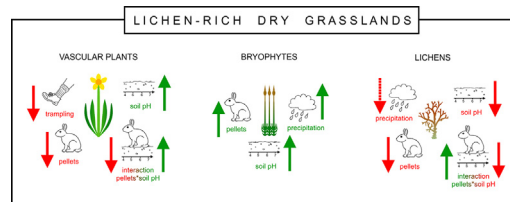
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HIGHLIGHTS

- We explored the multitaxon effects of disturbance on lichen-rich dry grasslands.
- We evaluated the impact of human trampling and eutrophication by an alien herbivore.
- We found a soil-dependent effect of the alien herbivore on multiple taxa.

GRAPHICAL ABSTRACT



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ABSTRACT

Dry grasslands are listed among the habitats of conservation concern in Europe. Here, based on a multitaxon approach including vascular plants, bryophytes and lichens, we explored the effects of small-scale disturbance on lichen-rich dry grassland vegetation by surveying 60 sites across the Po Plain (Northern Italy). In particular, we evaluated the impact of human trampling and fecal pellet deposition by the alien invasive herbivore *Sylvilagus floridanus*. We found a soil-dependent response of multiple taxa to the impact of the herbivore. For plants, beside a negative effect of trampling, the interaction between fecal pellet amount and soil pH indicates that the negative effect of the invasive herbivore is stronger on acidic soils. Bryophyte cover increased with increasing soil pH, annual rainfall and fecal pellet, while it was not affected by trampling. Lichen richness and cover decreased with increasing soil pH. The marginal interaction between soil pH and amount of fecal pellet indicates that the more negative effects on lichens may be expected on calcareous soils. Trampling did not affect lichen patterns and the rainfall gradient marginally affected lichen cover with a negative effect. Lichen species richness is also negatively affected by increasing vascular plant cover. The main implications of this study for improving conservation are: (1) conservation practices should be tailored to organism and substrate type; (2) bryophyte and lichen diversity patterns are influenced also by climatic conditions, suggesting that the impact on these organisms may be exacerbated by climate change; and (3) strict conservation, even through active exclusion of wild fauna, of the most species-rich sites should be recommended, even if previous literature and the negative plant cover-lichen richness relationship found in this study indicate that moderate mechanical disturbance could be a practical tool to enhance cryptogams.

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1. Introduction

Dry grasslands are important habitats for biodiversity conservation, hosting several rare species and species-rich communities of plants,

invertebrates (Schirmel et al., 2014; Zulka et al., 2014), and vertebrates (Goriup et al., 1991). Furthermore, they host terricolous cryptogams, mostly lichens (lichen-rich dry grasslands) and bryophytes that greatly contribute to ecosystem functioning in arid environments (Maestre et al., 2011; Zedda and Rambold, 2015). In Europe, dry grasslands on both siliceous (acidic) and calcareous (basic) substrates are listed among habitats of conservation concern according to the Habitat

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Directive (92/43/EEC; Jentsch and Beyschlag, 2003), being threatened by multiple impacts.

Large-scale impacts include habitat loss and fragmentation (Jentsch and Beyschlag, 2003), atmospheric nitrogen deposition (Sparrius et al., 2013; Stevens et al., 2012), and climate change (Jones, 1997). Small-scale impacts are mainly related to invasive plant species (Assini, 2008), overgrazing (Kohyani et al., 2008a, 2008b), and mechanical disturbance. In particular, human trampling usually impacts vascular plants, whose sensitiveness depends on the biological growth form (Pescott and Stewart, 2014), and fruticose lichens that are the most sensitive group among cryptogams (Jägerbrand and Alatalo, 2015; Grabherr, 1982). However, a moderate trampling could even enhance the local dispersal of vegetative propagules of terricolous lichens (Heinken, 1999).

Beside humans, herbivores also may contribute to trampling, even if their impact on natural and semi-natural vegetation (Pascual et al., 2017) is mainly associated with overgrazing (Kohyani et al., 2008a, 2008b) whose effects include soil eutrophication (Jentsch and Beyschlag, 2003). Eutrophication is among the most important factors threatening plant diversity of herbaceous plant communities worldwide (Soons et al., 2017; Storkey et al., 2015), being highly detrimental also to lichens (Southon et al., 2012; Sparrius et al., 2013), with direct negative effects on their eco-physiology (Stevens et al., 2012) and community composition (Giordani et al., 2014).

Previous research carried out in the dry grasslands of the western Po Plain (Assini, 2008) indicated that the activity of the alien invasive herbivore rabbit *Sylvilagus floridanus* can potentially threaten native vegetation by eutrophication related to fecal pellet deposition (Clark et al., 2005). This species, native to North America, was introduced in 1966 near Turin for hunting purposes, and quickly invaded the Po Plain in Piedmont and western Lombardy (Trocchi and Riga, 2005; Angelici and Spagnesi, 2008), forming dense populations in marginal habitats, such in the case of lichen-rich dry grasslands. However, the negative effects of this herbivore on lichen-rich dry grasslands have been never evaluated.

The impact of trampling and soil eutrophication can vary according with soil pH. For example, Stevens et al. (2010), demonstrated that the negative effects of eutrophication are exacerbated by increasing soil acidity. Also Löbel et al. (2006) showed that the interaction between environmental factors and soil pH could significantly affect species richness in lichen-rich dry grasslands vegetation. However, these interactive effects could differ among different organism groups composing the vegetation of dry grasslands. In this perspective, the multi-taxon approach is increasingly adopted to assess the effects of disturbance in natural and semi-natural habitats (Grabherr, 1982; Löbel et al., 2006; Nascimbene et al., 2014; Zulka et al., 2014; Jägerbrand and Alatalo, 2015). The simultaneous assessment of the response of multiple taxa to disturbance could therefore provide more robust information on biodiversity patterns and support more effective conservation compared to focusing on a single taxon. Despite the fact that in dry grasslands, beside vascular plants, both lichens and bryophytes may significantly contribute to ecosystem biodiversity and functioning (Maestre et al., 2011; Zedda and Rambold, 2015), these organisms are still largely overlooked in conservation policies.

This work aims at exploring the effects of small-scale disturbances on lichen-rich dry grasslands on both acidic and calcareous soils. In particular, our multi-taxon approach tested: (1) the influence of trampling and fecal pellet deposition, assumed as proxy for eutrophication (Clark et al., 2005) by the alien invasive herbivore *Sylvilagus floridanus* on species richness and cover of vascular plants, lichens and bryophytes; (2) whether the effects of these disturbances vary depending on soil pH. Since the spatial distribution of our sites spanned a relatively large rainfall gradient, we also tested (3) the effect of climate on the three taxonomical groups. Due to their different ecological requirements and traits, the three taxa are expected to exhibit contrasting responses to disturbance that can be mediated by soil pH. In general, we expect

that in our species-rich habitats cover and/or species richness decreases with increasing disturbance, and that this relationship could be modified by a taxon-specific interactive effect with soil pH. Moreover, due to their poikilohydric behavior (Green and Lange, 1995), we expect that the patterns of lichens and bryophytes would be influenced also by rainfall, while this factor should not influence vascular plants due to the strong drainage capacity of the soils that may offset the effects of the rainfall gradient. Finally (4), we also accounted for the potential effect of vascular plant cover on bryophytes and lichens testing the hypothesis that increased vascular plant cover can outcompete lichen and bryophyte species (Alatalo et al., 2017; Jägerbrand et al., 2012).

2. Materials and methods

2.1. Study area

The study was carried out in the central-western Po Plain, from the area surrounding Turin to the boundary between Lombardy and Veneto. Mean annual temperature ranges between 11 °C and 13.5 °C, and annual rainfall ranges between 600 mm and 1200 mm. Soil pH ranges from very acidic and acidic (pH = 4–5, north of the Po river) to subneutral (pH = 6, near the Po river), and basic (pH = 7, south of the Po river).

In this area, lichen-rich dry grasslands are at the southernmost edge of their range (Assini et al., 2013; Gheza, 2015). This habitat is extremely fragmented and the few remnants are usually located in marginal, unproductive areas along rivers and are not actively managed. Interviews to Natural Park's managers carried out preliminarily to this study revealed that these fragments are only locally and sporadically used for human activities (e.g. trekking, biking, hunting, grazing). On the other hand, this condition increases their suitability for small-sized wild animals, including the alien invasive *Sylvilagus floridanus*, while larger herbivores (i.e. wild boar, *Sus scrofa*) only sporadically feed in these habitats.

2.2. Site selection

Across the study area, we performed a preliminary site selection checking the available maps in order to find all the areas with natural and semi-natural lichen-rich dry grasslands. This process resulted in 12 areas distributed along the main river valleys: Ticino, Sesia, Dora Baltea, Stura di Demonte, Po, Orba, Scrivia, Lambro, Adda, Brembo, Serio and Oglio, and one site in the Lomellina area. In these areas, lichen-rich dry grassland sites were identified by analyzing GIS maps and thanks to the cooperation with local botanists and Park managers. The sites preliminarily identified were then inspected during winter 2015–2016 in order to evaluate their suitability for this study. Dry grasslands in rather pioneer dynamic stages and hosting cryptogams were considered suitable, while sites in more mature stages of the successions, characterized by well-developed soils and absence of cryptogams, were considered unsuitable. Overall, 84 grasslands sites were inspected and only 60 resulted suitable (Appendix A). All these grasslands can be labeled under the EU habitat codes 2330 ("Inland dunes with open *Corynephorus* and *Agrostis* grasslands") and 6210 ("Semi-natural dry grasslands and scrubland facies on calcareous substrates"). The suitable grassland sites are evenly distributed in Lomellina, Ticino, Sesia, Po, Orba, Scrivia, Serio; 55 are included in Regional Parks and/or Sites of Community Importance (SCI) according to the European Habitat Directive, while five are located outside protected areas. For each grassland site, mean annual precipitation was retrieved from the website of the Regional Environmental Agencies of Piedmont (www.arpa.piemonte.gov.it) and Lombardy (www2.arpalombardia.it), using the values of the nearest meteorological station.

2.3. Sampling design

Vegetation, including vascular plants, lichens and bryophytes, was surveyed between April and June 2016 in 3 m radius circular plots. In each grassland site, the number of plots was proportional to the grassland area: 1 plot for sites between 100 and 1000 m²; 2 plots between 1001 and 3000 m²; 3 plots between 3001 and 5000 m²; 5 plots between 5001 and 20,000 m²; and 7 plots for areas larger than 20,000 m². This resulted in a total of 185 plots (Appendix A). In each site, plots were placed at regular spatial spans along the linear transect placed between the two furthest vertices of the grassland. This procedure was performed using Qgis (Qgis Development Team, 2009).

In each plot, the cover (%) and the mean height of the five vegetation layers (arboreal, higher-shrubby, lower-shrubby, herbaceous, cryptogamic) were recorded, as well as the cover of each plant, lichen and bryophyte species. Most species were identified in the Laboratory of Flora, Vegetation and Ecosystem Services of the University of Pavia, where voucher specimens are stored. Several lichen specimens, identifiable only on the basis of chemical analyses, were checked with thin-layer chromatography for secondary metabolites. Critical bryophyte specimens were checked by an expert bryologist. Nomenclature follows Tison and de Foucault (2014) for vascular plants, Nimis (2016) for lichens, and Cortini Pedrotti (2001) for bryophytes.

Soil pH was measured in the field with a portable kit within each plot in a position not contaminated by the occurrence of fecal pellets. In each plot, we also recorded: 1) the overall human trampling, estimated according to a categorical scale: 0 (no trampling), 1 (<5 m² showing evidence of trampling on vegetation and/or bare soil), 2 (5–10 m²), 3 (10–15 m²), 4 (>15 m²); 2) fecal pellet abundance of the invasive *S. floridanus* estimated according to a categorical scale: 0 (no pellet), 1 (<2 pellet/m²), 2 (3–5 pellet/m²), 3 (>5 pellet/m²). Fecal pellet of this herbivore are easily identifiable in the field from those of *Lepus europaeus* but are rather similar to those of *Oryctolagus cuniculus*. In this case, the attribution to *S. floridanus* was based on the direct observation of *S. floridanus* individuals in absence of both *O. cuniculus* individuals and holes (typically made by this species) in the whole site. To back this, the current distribution of *S. floridanus* was checked in detail, not only by means of published literature (Angelici and Spagnesi, 2008), but also through interviews with Park keepers, gamekeepers and zoologists with good knowledge of the wildlife occurring in our study sites. According with Clark et al. (2005), the amount of fecal pellet was used as a proxy for soil eutrophication. During the fieldwork we also quantified grazing activity as well as boar rooting. However, these disturbances were found in only a few plots and their effect was therefore no longer considered.

2.4. Data analysis

The effects of the independent explanatory variables (Appendix B) on the three taxa were analyzed using general linear mixed-effect models. The response variables were: 1) vascular plant species richness and cover; 2) lichen species richness and cover; 3) bryophyte species richness and cover; 4) species richness and cover of alien vascular plants; 5) species richness and cover of plants, lichens, and bryophytes of conservation concern according to European (Habitat Directive) and National regulations. We used a Poisson distribution for species richness and a normal distribution for cover data. To make estimates comparable across predictors, the explanatory variables were standardized to mean 0 and standard deviation 0.5 (Gelman, 2008). All models included all the plots ($n = 185$) nested within the sites ($n = 60$) as random factors. This random structure accounted for the spatial dependence in the sampling design.

The full model included the following variables:

Response variable (species richness or cover)

~ pH + pellet + trampling + pellet × pH + pH × trampling + rainfall

The full models were simplified with a backward deletion procedure ($p < 0.05$). P-values ranging between 0.05 and 0.1 were retained as indicative of marginal effects. The use of model selection based on p-values in ecological studies has been widely debated in recent years (Johnson and Omland, 2004; Gelman, 2013). However, the best approach to analyze complex ecological data has still to be found (Murtaugh, 2014). The traditional null hypothesis testing approach (p-values selection) is still effectively used to test biological accurate hypotheses in studies characterized by low collinearity (Gelman, 2013; Murtaugh, 2014). All analyses were performed using R3.4.1 (R Core Team, 2015). For the linear mixed-effects model analyses the packages “lme4” (Bates et al., 2014) and “nlme” (Pinheiro et al., 2013) were used.

We also performed a model selection using an information theoretic approach to evaluate alternative competing models involving the variables included in the models explained above. Our information-theoretic approach compared the fit of all the possible candidate models nested within the full models (Burnham and Anderson, 2002). Models were fitted using the maximum likelihood method. The fit of each model in the set was then evaluated using second-order Akaike's information criterion (AICc). The best fit is indicated by AICc_{MIN}, the lowest value of AICc. In a set of n models each model i can be ranked using its difference in AICc score with the best-fitting model ($\Delta AICc_i = AICc_i - AICc_{MIN}$). A model in a set can be considered plausible if its $\Delta AICc$ is below 2 (Burnham and Anderson, 2002). We also computed the model weight (w_i) as the weight of evidence in favour of each model. The weights w_i represent the relative likelihood of a model. For each model, we first calculated its likelihood as $\exp(-0.5 * \Delta AICc_i)$. The weight w_i for a model is its likelihood divided by the sum of the likelihoods across all models. The multi-model inference analyses were performed using the ‘MuMIn’ package implemented in R version 2.13.0 using the functions `dredge()`, `model.avg()` and `confint()`. Since the results from the traditional p-value based analyses and the multi-model inference converged, we present only the former in the main text while the latter are reported in supplementary materials (Appendix C).

As the three taxa are expected to respond to the same environmental factors we could not include them as predictors in the environmental model described above. However, the relationship between vascular plant cover and lichens and bryophytes was tested by a simple regression model.

3. Results

A total of 255 vascular plants, 32 lichens and 15 bryophytes were recorded in 185 plots (Appendix D). They included 17 alien vascular plants: two archaeophytes (species introduced before the year 1492) and 15 neophytes (species introduced after the year 1492) (Celesti-Grapow et al., 2010). Nine vascular plants, one lichen (*Cladonia portentosa* (Dufour) Coem.) and one bryophyte (*Leucobryum glaucum* (Hedwig) Ångström) are species of conservation concern according to Regional, National and/or European policies.

The explanatory variables included in the model did not affect neither species richness nor cover of both the species of conservation concern and alien species (data not shown). In contrast, trampling and fecal pellet amount and/or their interactions with soil pH (ranging between 4 and 7) significantly affected the cover and/or species richness of the three organism groups (Table 1).

Trampling had a negative effect on vascular plant cover regardless of soil pH. On the other hand, cover of vascular plants increased at the increase of soil pH and decreased at the increase of fecal pellet amount, irrespectively of soil pH. In contrast, the interaction between fecal pellet and soil pH was significant for species richness, indicating that the negative effect of the invasive herbivore is stronger on acidic than on calcareous soils (Fig. 1a). Rainfall did not affect nor species richness, neither cover of vascular plants.

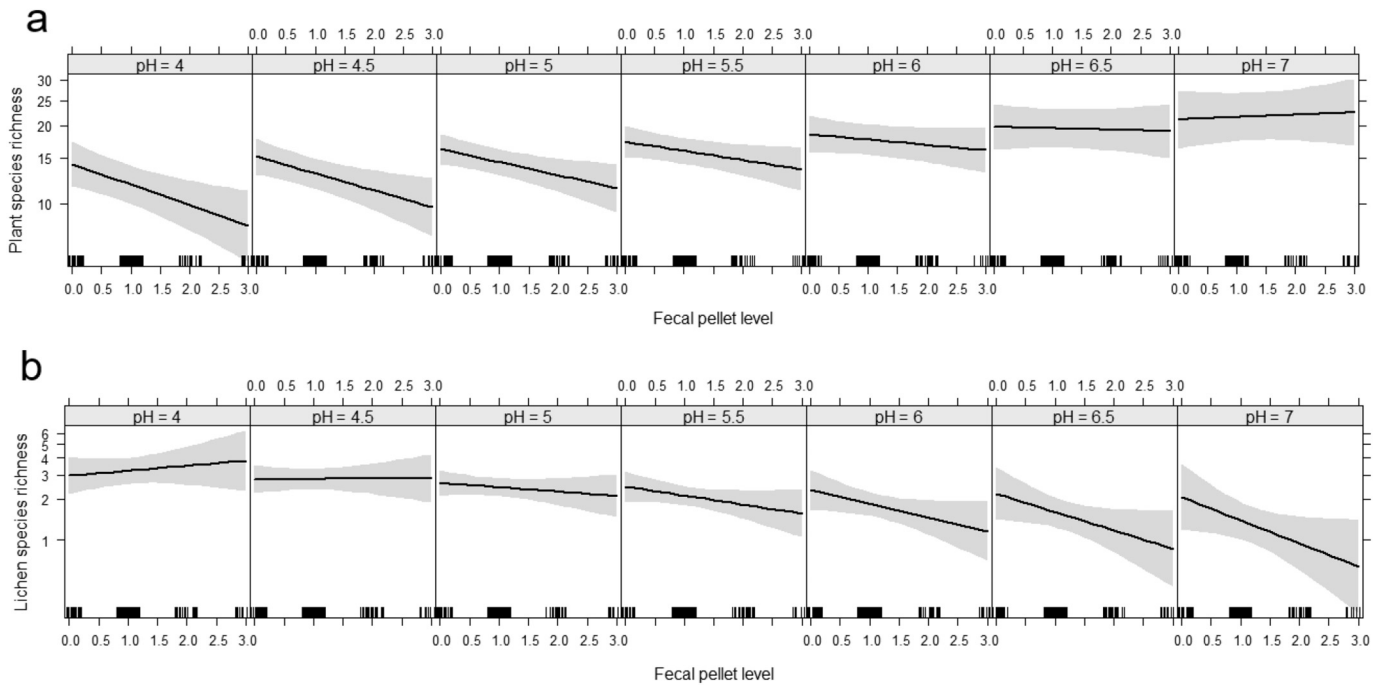


Fig. 1. Interactive effect between soil pH and the fecal pellet levels by the alien invasive herbivore *Sylvilagus floridanus* on (a) plant species richness and (b) lichen species richness.

Bryophyte species richness did not respond to the local variables tested in this study. In contrast, bryophyte cover increased with increasing soil pH, mean annual rainfall (Fig. 2a), and fecal pellet, while it was not affected by trampling (Table 1). Plant cover did not influence bryophyte richness (Fig. 3a) and cover (not shown).

Lichen richness and cover decreased with increasing soil pH. Species richness was negatively affected also by increasing fecal pellet (Table 1). Lichen richness was also marginally affected by the interaction between soil pH and fecal pellet with a contrasting pattern as compared with that of vascular plants: fecal pellet produced more negative effects on lichens on calcareous soils than on acidic soils (Fig. 1b). Similarly to bryophytes, trampling did not affect lichen patterns, while rainfall had a marginal negative effect on lichen cover (Fig. 2b). Plant cover negatively affected lichen richness (Fig. 3b) while it did not influence lichen cover (not shown).

4. Discussion

While only vascular plants were negatively affected by human trampling, our study provides support for a soil-dependent response of multiple taxa to the impact of the invasive herbivore *Sylvilagus floridanus* in lichen-rich dry grasslands. However, contrasting patterns were found among plants, bryophytes and lichens, confirming the view that the response to disturbance may differ among organisms with different traits and ecological requirements (Poschlod et al., 2005; Löbel et al., 2006) and stressing the importance of multiple taxa assessment to support science-based conservation.

In contrast with several previous studies (e.g. Grabherr, 1982; Jägerbrand and Alatalo, 2015), in our lichen-rich dry grasslands the moderate intensity of human disturbance and the rarity of large wild herbivores are likely responsible for the lack of impact of trampling on

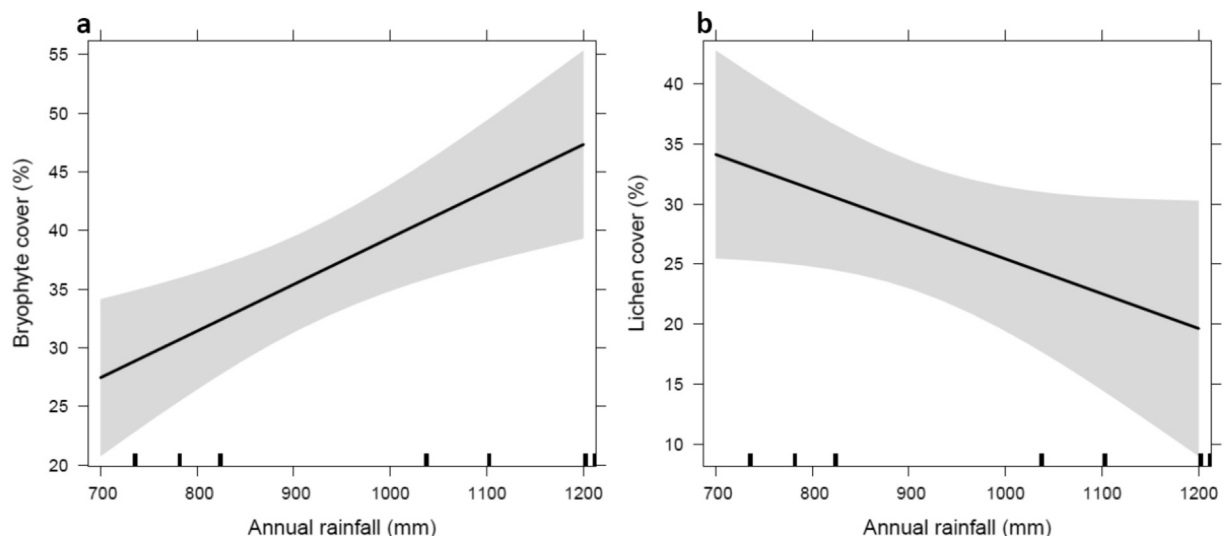


Fig. 2. Relationship between annual rainfall (mm) and (a) bryophyte, and (b) lichen species richness.

Table 1

Final models of each response variable (species richness and cover for each taxonomical group). Only the significant explanatory factors and their interactions are shown after a backward deletion procedure ($P > 0.05$).

		Species richness			Cover		
		Estimate	Std Error	p-value	Estimate	Std Error	p-value
Vascular plants	pH	0.43407	0.11181	0.0001	22.60310	4.162971	<0.0001
	Fecal pellet	-0.14541	0.06088	0.0169	-6.54439	2.540168	0.0114
	Trampling				-5.62896	2.263655	0.0142
	Precipitation						
	Fecal pellet*pH	0.22391	0.10600	0.0346			
Bryophytes	pH*Trampling						
	pH				13.95643	4.647144	0.0032
	Fecal pellet				11.32829	3.520046	0.0016
	Trampling						
	Precipitation				15.49566	4.535219	0.0012
Lichens	Fecal pellet*pH						
	pH*Trampling						
	pH	-0.60841	0.15744	0.0001	-27.1672	6.022182	<0.0001
	Fecal pellet	-0.18477	0.13592	0.1740			
	Trampling						
	Precipitation				-11.6677	6.016371	0.0575
	Fecal pellet*pH	-0.51635	0.28967	0.0747			
	pH*Trampling						

bryophytes and lichens. A moderate trampling, that implies mechanical soil disturbance, could even positively affect these components of dry grasslands vegetation, contributing to form gaps in which (re-)colonization by pioneers can take place. Moderate trampling could also positively affect the dispersal of lichen fragments, which are effective propagules for local colonization (Heinken, 1999). On the other hand, the impact of trampling on vascular plant cover may corroborate the view that a moderate disturbance regime could be useful for the maintenance of lichen (and bryophyte)-rich vegetation, hindering the development of a continuous layer of vascular plant vegetation (Alatalo et al., 2017). The negative relationship found in this study between plant cover and lichen richness would support this hypothesis. This threshold between disturbance intensity and cryptogam development could be a reference for active conservation aiming at maximizing the co-occurrence of lichens, bryophytes and vascular plants in dry grasslands.

Moderate trampling could be even provided by small-sized herbivores such as the alien invasive *S. floridanus*. Our results highlight that the impact of this invasive herbivore on dry grassland vegetation is taxon- and soil-dependent with contrasting patterns among vascular plants, lichens and bryophytes. This impact is probably more related to eutrophication, associated with fecal pellet deposition, rather than to grazing and trampling, due to the small size of the species (Bakker

et al., 2006). For vascular plant richness, the negative impact of the invasive herbivore was exacerbated on acidic soils, where plant communities have usually lower diversity and cover and are probably less productive. This pattern could fit with an eutrophication effect. For example, Storkey et al. (2015) suggested that nitrogen addition may impact plant diversity more heavily in acidic, compared to calcareous sites (see also Stevens et al., 2010). Under these circumstances, eutrophication could also impact ecosystem functioning by reducing plant cover with potential negative effects on the stability of vegetation productivity (Wang et al., 2017). This hypothesis is corroborated by the negative effect of pellet amount on vascular plant cover. For lichens, the marginal interactive effect of fecal pellet amount with soil pH had an opposite pattern compared with that of vascular plants, predicting a stronger impact of the invasive herbivore on calcareous dry grasslands, where lichen cover is lower. Also bryophyte cover is influenced by the impact of the invasive herbivore and soil pH. The positive effect of fecal pellet amount, as well as of increasing soil pH, suggest that in calcareous dry grasslands bryophytes may compensate the low contribution of lichens and the impact of eutrophication on plant diversity.

According with our expectations, both bryophytes and lichens were influenced by rainfall, even if with contrasting patterns. The positive effect of rainfall on bryophyte cover reflects their affinity to humid

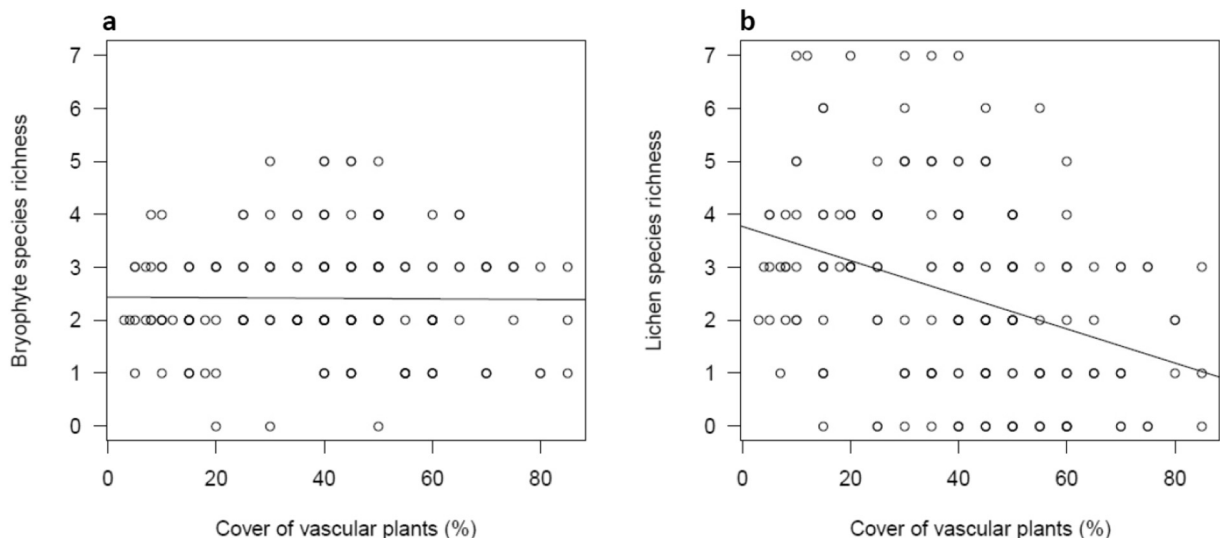


Fig. 3. Relationship between the cover of vascular plants (%) and (a) bryophyte, and (b) lichen species richness.

situations, their metabolic and ontogenetic activity being enhanced by water availability (Goffinet and Shaw, 2008). In general, this framework could apply also to lichens, whose metabolism depends on thallus hydration (Green and Lange, 1995). However, water availability may differently affect lichens, depending on their thallus growth form. For example, fruticose-filamentous species are hindered by excessive wetting that depresses net assimilation (Coxson and Coyle, 2003). This could happen also for several tiny fruticose species composing lichen communities in dry grasslands that may be scarcely tolerant to prolonged thallus inundation. Moreover, high rainfall may disadvantage lichens due to their scarce competitiveness with the more fast-growing bryophytes.

5. Conclusions

Results of this study provide key implications for improving biodiversity conservation in lichen-rich dry grasslands: (1) the contrasting patterns among different taxa in relation to disturbance highlight the usefulness of the multi-taxon approach in which overlooked organisms, such as bryophytes and lichens, are included in the assessment of the impacts on biodiversity (Grabherr, 1982; Löbel et al., 2006; Jägerbrand and Alatalo, 2015). While these organisms are likely to greatly contribute to dry grasslands biodiversity and functioning (e.g. Jentsch and Beyschlag, 2003; Maestre et al., 2011), being also associated to relevant ecosystem services (e.g. Zedda and Rambold, 2015), their diversity patterns in relation to disturbance have thus far been overlooked. (2) Conservation practices should be tailored to organism (Socolar et al., 2016) and substrate type, beside the general prediction that the most vulnerable conditions should be expected where vegetation cover is lower. In particular, results suggest that for vascular plant conservation efforts should be mainly assigned to acidic dry grasslands where they are expected to be less competitive and resilient. For similar reasons, priority for lichen conservation should be assigned to calcareous dry grasslands. On the other hand, calcareous and acidic sites host the highest richness of plants and lichens respectively, being therefore alternatively important to maximize the conservation of the regional species pool of these two taxa. This implies that, at the landscape level, patches of dry grassland should be protected on both acidic and calcareous soils. (3) While vascular plants are influenced mainly by local disturbance in interaction with soil pH, bryophyte and lichen patterns are influenced also by climatic conditions, suggesting that the local impacts on these organisms may be exacerbated by climate change. Increasing aridity may negatively affect bryophytes, while intensification of rain events may hinder lichen development, especially for inundation intolerant species. (4) Besides the threats already posed by the alien herbivore *S. floridanus* to the native wild fauna (Trocchi and Riga, 2005; Angelici and Spagnesi, 2008), this invasive species may also negatively affect plant and lichen diversity in lichen-rich dry grasslands. In this context, active habitat management is the main tool available to mitigate the impact by invasive fauna (see e.g. Barrios-Garcia and Ballari, 2012 for wild boars) and strict conservation, even through active exclusion of wild fauna, of the most species-rich sites should be recommended. However, previous literature (e.g. Dostalek and Frantik, 2008) and the negative plant cover-lichen richness relationship found in this study indicate that moderate mechanical disturbance could be a practical tool to locally enhance the occurrence of cryptogams within plant-dominated stands.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.05.191>.

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